Dispersal patterns and survival of Atlantic salmon (Salmo salar L.) juveniles in a nursery stream

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The spatial and temporal patterns of dispersal and the survival of Atlantic salmon (Salmo salar L.) fry and parr were analysed over 1 year in a small stream of the Basque Country (south-west France). Dispersal just after emergence was studied with eight drift nets placed 10 to 800 m downstream from an artificial redd stocked with 15 000 eyed eggs. Subsequent distribution of parr was determined by electrofishing in June, October, and February in representative sections of the stream including habitats 750 m upstream and 2400 m downstream from the redd. Early dispersal following emergence lasted 12 days for the majority (95%) of the fry population. Most fry (71%) settled within the first 200 m downstream from the redd, and 91% within the first 400 m. In June, parr were found 2400 m downstream and 750 m upstream, with 68% of the population established within 900 m downstream, and only 4% upstream. In October, there was a slight downstream shift of densities. In February, 56% of the parr were found within 900 m downstream and 11% upstream. Survival from egg planting to first dispersal in March was 51.9% and 11.8% over 1 year.

Key words: salmon juvenile, dispersion, mortality.

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Introduction

It is generally held that dispersal of Atlantic salmon at emergence from the redd is limited (Egglishaw and Shackley, 1973; Kennedy, 1982, 1988; Gustafson-Marjanen and Dowse, 1983). Fry exhibit territorial behaviour soon after emergence (Kalleberg, 1958), which leads to a gradual dispersal from the redds (Le Cren, 1973). Hay (1989) reported that dispersal of fry from one isolated redd during a 4-week period was considerable and ranged over several hundred metres upstream and downstream. In an experiment in a 50-m section of an artificial stream channel, Marty and Beall (1989) found a massive downstream displacement of fry occurring in a short time, with over 50% of the fry population leaving the experimental section. Dispersal can be extensive for wild parr from a single spawning area (Vallieres and Dulude, 1990) and for hatcheryreared salmon part released in summer (Elson, 1957). In our experiment we planned to study the patterns of dispersal and survival of wild salmon juveniles at emergence and during the following year in a natural stream system with no indigenous salmon, and, in particular, determine the extreme range of dispersal and its precise timing over a 1-year period.

Materials and methods

Study site

The experiment was conducted in the Lapitxuri Brook, a tributary of the River Nivelle (Fig. 1) at the France-Spain border, in the Basque Country. The Lapitxuri flows through a wooded watershed (mostly oak, chestnut, and alder) on primary layers of schist and quartzite (see Marty et al., 1986, for more details). Water temperatures vary between 4 and 21°C and flows between 0.06 and 10 m³ s⁻¹. During the early part of the study (March), discharge stayed between 0.39 and 0.51 m³ s⁻¹ and temperatures between 7 and 14.5°C. No salmon occur naturally in this part of the catchment, but there is a population of brown trout (Salmo trutta L.). Eel (Anguilla anguilla L.), minnow (Phoxinus phoxinus L.), stone loach (Noemacheilus barbatulus L.), and lamprey (Lampetra planneri Bloch) are other common species.

The study area was located between the INRA experimental station and the confluence with the

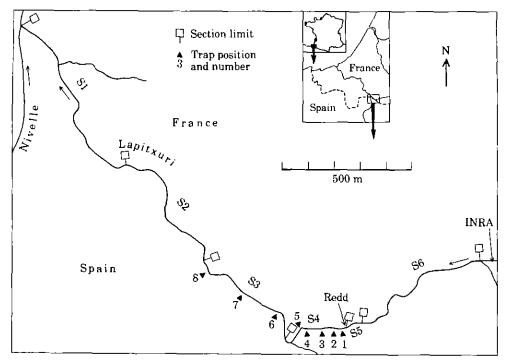


Figure 1. Situation of the study site in the Lapitxuri Brook, tributary of the River Nivelle in south-west France. Positions of the traps and limits of sections used for electrofishing inventories are indicated.

Table 1. Characteristics of experimental sections and number and proportion of representative subsections used during the three electrofishing surveys in the Lapitxuri Brook.

Section	Length (m)				Subsections used for electrofishing					
			Area			June 1989	Oct 1989 and Feb 1989			
		m²	Per cent rapid-riffle	Per cent flat	No.	Per cent of area	No.	Per cent of area		
6	700	3 419	62.0	38.0		6.2	2	4.4		
5	50	345	58.0	42.0	4	100.0	4	100.0		
4	300	1 406	72.1	27.9	12	74.9	5	24.0		
3	600	2 733	60.2	39.8	7	22.9	7	20.0		
2	700	3 951	61.6	38.4	4	12.0	2	5.0		
l	800	4 502	57.7	42.3	2	6.0	3	6.4		
Total	3150	16 356			31		23			

Nivelle (Fig. 1). Its total length was 3150 m, with an average width of 5.2 m (range 3 to 8 m) and a slope of 11%. It was divided into six contiguous sections of different lengths (50 to 800 m; Fig. 1, Table 1). Sections located on either side of the site selected to establish the artificial redd were the shortest in order to appreciate better the high-density gradient expected to be found in this zone. Habitats were characterized and quantified according to morphological and physical criteria (water velocity and depth, substratum quality) in November 1988. Two types of habitat were identified in each section: rapid-riffle (water velocity

>0.4 m s⁻¹, depth<0.35 m, substratum composed of pebbles, stones, and boulders) which represented 57–72% of the surface area in the different sections, and flats (water velocity<0.4 m s⁻¹, depth 0.3–0.6 m, substratum of small pebbles, gravel, sand, and silt) which represented 30–43% of the surface area (Table 1). Pools (depth>0.6 m) which covered less than 1% of the total surface were included in the flats. The artificial redd was established between the upstream end of a homogenous riffle zone, 180 m long, which constituted the upstream part of section 4 and a 10-m-long flat which formed the downstream end of section 5.

The redd (=point 0) was located 740 m downstream from the INRA experimental station and 2400 m upstream from the confluence of the Lapitxuri with the Nivelle (Fig. 1).

Biological material

Eggs were collected from the Nivelle wild salmon stock on 7 December 1988, fertilized with sperm from males of the same stock and incubated at the INRA hatchery. A group of 15 000 eyed eggs was sorted and counted, placed in Vibert boxes, and buried on 15 February 1989 in a single artificial redd excavated at the upstream end of the selected stretch (Fig. 1).

Emergence and early downstream dispersal

Dispersal of downstream drifting or moving fry just after emergence was monitored with modified tyke nets at the end of which wooden live boxes were attached. The bottom of the frame supporting the net was buried in the substratum and the whole water column was sampled. Each net, made of nylon netting with 3-mm mesh opening, had the following dimensions: length, 1.65 m; height, 0.38 m; width at the upstream end, 0.25-0.5 m, adjustable according to the desired water flow. The flow filtered by each net was targeted to reach a relatively low value of 5% of the total discharge, in order to be able to operate as long as possible in high-velocity water $(0.6-0.7 \text{ m/s}^{-1})$ and to sample downstream drifting or moving fry without affecting too much the fry population size. The filtering capacity of each net was estimated with three to 11 velocity and depth measurements made along a transect in front of the opening. On 13 March, nets were placed 12, 47, 86, 148, 205, 394, 591, and 789 m downstream from the redd. Trap sites were selected in order to have comparable conditions between traps concerning depth (no greater than 0.3 m, because of net frame height), distance from the bank (1.5 m minimum to avoid turbulences), and substratum profiles (areas with major obstacles such as boulders or logs were avoided). The entrance of nets were placed near or in the main flow, where velocities of 0.50 to 0.70 m s⁻¹ corresponded to the average velocity of the transect. No attempt was made to determine upstream movement at this early stage.

Starting on 13 March, traps were visited every morning and the fry enumerated and removed to the INRA hatchery. Samples of fry were collected every 5 days and preserved in 4% formalin for further analysis (length, weight, stomach content). Trapping was interrupted on 4 April by a spate. Because the number of fry caught was low, we assumed that it occurred at the end of the initial dispersal phase (Marty and Beall, 1987, 1989). The nets could not be replaced due to the high water conditions that prevailed thereafter.

Estimate of the downstream moving population

The number of downstream drifting or moving fry passing by the i_{th} trap (Ne_i) were estimated by the daily fry captures in the trap (N_i) , divided by the average percentage of total flow filtered by the trap (q_i) according to the formula: $Ne_i = N_i/q_i$. The following assumptions were made: fry were randomly distributed in the water column across the stream width when migrating downstream and there was no net avoidance behaviour. After entry, the fry could not escape from the net due to the trap design and the high water velocities.

Estimate of the resident fry population

The numbers of resident fry in a section were analysed by the differences between the estimated numbers of fry passing at successive traps (i and i+1) minus the number of fry captured and removed (N_i) : $Nr_{(i,i+1)} = Ne_i - Ne_{(i+1)} - N_i$. Because it was impossible to estimate, we did not take into account mortalities due to predation or competition, which may have occurred during this period.

Distribution of parr

Electrofishing population inventories were conducted around the median dates of 14 June 1989, 10 October 1989, and 28 February 1990. The De Lury method (Seber and Le Cren, 1967) was used (two-four runs in June, two runs in October and February) in sample subsections ranging in size from 71 to 191 m², each representative of one of the two types of biotopes in each of the six sections of stream considered. Thirty-one subsections were electrofished in June. They represented 6 to 100% of the area of each section. Their number was reduced to 23 (including an additional subsection in section 1) in the October and February inventories, with 4.4 to 100% of the area sampled (Table 1). Fish were anaesthetized with ethyleneglycol monophenyl ether and measured to the nearest mm (fork length). Weights to the nearest 0.1 g were taken on fish in each sampled subsection. After handling, fish were released in their original subsection, and distributed over its whole surface.

Estimates of populations (Pi) and of their variances (si²) were computed for each subsection according to the method of Seber and Le Cren (1967) and were considered as independent. In order to homogenize computations on variances, the first two runs only were used in the few cases where three or four runs were made in June. According to this method, confidence intervals of the estimates, for p=0.05, are symmetrical and are equal to t times the standard deviation. Estimates of populations established in a given section over biotopes of the same type (Pb), and then over the two types of biotopes

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Table 2. Number of fry captured in traps during the emergence and early dispersal period in spring of 1989 in the Lapitxuri Brook (T1=trap number 1; ...). Distance of trap downstream from redd in parentheses.

	T1 (12 m)	T2 (47 m)	T3 (86 m)	T4 (148 m)	T5 (205 m)	T6 (394 m)	T7 (591 m)	T8 (789 m)
13/3		0	0	0	0	0	0	0
14/3	0	0	0	0	0	0	0	0
15/3	0	l	0	0	0	0	0	0
16/3	1	0	0	0	0	0	0	0
17/3	0	0	0	0	0	0	0	0
18/3	0	0	l	0	2	0	0	0
19/3	2	0	0	0	0	0	0	0
20/3	0	0	1	1	0	0	0	0
21/3	1	0	0	0	0	0	0	0
22/3	2	0	1	0	0	0	0	0
23/3	5	10	4	0	0	0	0	0
24/3	20	14	17	5	2	0	0	0
25/3	38	23	16	4	5	1	2	0
26/3	44	37	17	14	8	2	0	0
27/3	45	37	28	4	6	0	0	0
28/3	38	65	22	15	4	2	0	0
29/3	39	53	69	28	22	13	3	0
30/3	27	42	36	11	17	3	2	1
31/3	19	21	30	10	13	3	1	0
1/4	12	28	36	12	22	3	4	0
2/4	9	11	25	5	5	1	5	0
3/4	3	7	11	8	7	5	2	0
4/4	6	8	3	0	0	0	0	0
Total	313	357	317	117	113	33	19	l

(Pz) in the same section, and finally over the whole experimental stream (P), were obtained according to the procedure described by Baglinière and Champigneulle (1986), using the following formulas: $Pb=\Sigma Pi \times k$, where k is the surface coefficient for one biotope type in a particular section (i.e. k=total biotope surface/sum of the surfaces of the sampled subsections), $Pz=\Sigma Pbi$, and $P=\Sigma Pz$.

Their respective variances (sb², sz², s²) were calculated thus: $sb^2 = \Sigma si^2 \times k^2$, $sz^2 = \Sigma sb^2$, $s^2 = \Sigma sz^2$.

Fishing efficiency of the total runs varied from 0.76 to 1 in June, 0.86 to 1 in October, and 0.82 to 1 in February.

Results

Emergence and early downstream dispersal

The daily captures are presented in Table 2. Duration of emergence until the removal of trap 1 on 4 April was 23 days (Table 2). The majority (95%) of captures occurred within 12 days (23 March to 2 April) in the traps closest to the redd (T1 to T3). The modal day of captures was 27 March in T1, 28 March in T2, 29 March from T3 to T6. The only fry found in T8 was captured on 30 March. This shows that downstream dispersal occurred very rapidly over the first 600 m downstream from the redd.

Captures in trap 1 gave the best estimate of survival from egg planting to emergence (Table 3). Since some fry may have settled between the redd and trap 1, an estimated number of 57 resident fry for this section, derived from estimated density of fish which had settled or disappeared in the area between trap 1 and trap 2, gave an estimated population size of 7785 fry surviving from egg planting to emergence and first dispersal (=1270 fry captured in traps and removed +6491 fry settled between the redd and trap 8+24 fry moving past trap 8, Table 3), i.e. a survival rate of 51.9%.

The estimated densities of fry settling at different distances from the redd (Fig. 2a) were not highest immediately around the redd, as may have been expected, but 90–150 m downstream, in a stretch of stream very similar to the redd area. An estimated 71% of surviving fry settled within the first 200 m downstream from the redd, with 59.4% in the 50–150-m zone (Table 3). About 91% of all fry were found within 400 m from the redd. During this early dispersal phase, very few fry (0.4%) travelled beyond the 800-m trap.

Fixed weights of samples of fry collected in traps T1, T2, and T3 on three different dates (24 March, 29 March, and 2 April) were significantly different between dates (ANOVA, F=12.43, p<0.0001) but not between traps on the same date (ANOVA, F=1.03, p=0.362). Mean fixed weights increased from 0.19 g on 24 March to 0.22 g on 2 April.

Table 3. Estimated flow rate through traps $(q_i, m^3 s^{-1})$, numbers of trapped and removed fry (N_i) , estimated numbers of fry arriving at the level of each trap (Ne_i) , numbers effectively passing each trap $(Ne_i - N_i)$, numbers $(Nr_{(i,i+1)})$ and percentage of fry settling between two consecutive traps.

Variables	Tt (12 m)	T2 (47 m)	T3 (86 m)	T4 (148 m)	T5 (205 m)	T6 (394 m)	T7 (591 m)	T8 (789 m)	Total
	0.0405	0.0492	0.0571	0.0407	0.0549	0.0495	0.0537	0.0400	
Ň,	313	357	317	117	113	33	19	1	1270
Ne;	7728	7251	5554	2874	2058	667	354	25	
Ne N.	7145	6894	5237	2757	1945	634	335	24†	
(Nr _(i, i+1)) Per cent	57*	164	1340	2363	699	1278	280	310	6491
of total resident fry	0.9	2.5	20.6	36.3	10.7	19.6	4.3	4.7	

^{*}The estimated number of resident fry between the redd and T1 was obtained by applying the density between T1 and T2 to the corresponding area.

Table 4. Number of (Pz with 95% CL) and percentage of salmon juveniles found at different distances from the redd in the Lapitxuri Brook at different dates.

Direction of		Distance from	14 Jun	1989	10 Oct	1989	28 Feb 1990	
movement	Section	redd (m)	Pz	Per cent	Pz	Per cent	Pz	Per cent
Upstream	6	50-750	91 ± 5	1.8	92 ± 9	3.7	128 ± 11	8.6
•	5	0-50	94 ± 7	1.9	60 ± 3	2.4	36 ± 5	2.4
Downstream	4	0-300	1602 ± 72	32.0	472 ± 46	18.9	271 ± 43	18.3
	3	300-900	1805 ± 126	36.1	1038 ± 48	41.4	554 ± 53	37.4
	2	900-1600	981 ± 99	19.6	725 ± 31	28.9	422 ± 36	28.5
	1	1600-2400	432 ± 64	8.6	118 ± 5	4.7	71 ± 6	4.8
Total			5005 ± 187	100	2505 ± 89	100	1482 ± 78	100

Distribution of parr

The total estimated population size in the study zone was 5005 parr in June, 2505 in October, and 1482 in February (Table 4), but a small fraction of the population could get established beyond its limits. In mid-June, the minimal estimate for part dispersal was 2400 m downstream from the redd (confluence with the Nivelle River, Fig. 1) and 750 m upstream. The majority (68.1%) remained within the first 900 m downstream; 87.7% were found within 1600 m downstream, while a small proportion (3.7%) settled upstream (Table 4). In October, distribution of part was slightly different: 60.3% were within 900 m downstream from the redd, 89.2% within 1600 m, and 6.1% upstream (Table 4). During winter, there were no major changes and in February, 55.7% of the population were found within 900 m downstream from the redd, 84.2% within 1600 m, and 11% upstream.

The highest densities were found over the first 300 m in June (114 parr 100 m⁻²; Fig. 2b). There was a shift downstream of the highest densities towards the 300–900-m zone in October (38 parr 100 m⁻²; Fig. 2c). The following February densities were still highest in the

same area (20.3 parr 100 m⁻²; Fig. 2d), with a clear tendency for a regular decrease in densities towards the upstream and downstream ends of this zone. The increase in densities in the upstream stretch (2.7 parr 100 m⁻² in June and October, 3.7 fish in February) indicated an active upstream movement of juvenile salmon during the winter period.

The mean sizes (with 95% CL) of parr in the Lapitxuri Brook was 28 ± 0.2 mm in April, 50.5 ± 0.6 mm in June, 74.1 ± 14 mm in October, and 89.3 ± 2 mm in February. The growth of this salmon population was slower than in the Nivelle River where in October of the same year the sizes were 96.7 ± 2.3 mm in the upper reaches and 99.0 ± 2.2 mm in the lower reaches.

Numbers of fish decreased regularly over the year. Since fry captured in the traps were removed from the population, we corrected the number of planted eggs to estimate survival to the different dates of electrofishing. The removed fry (1270) correspond to 2447 eggs planted with a 51.9% survival rate. Thus, the corrected number of eggs planted is equal to 12 553 (15 000–2447). Survival estimates from egg planting to the June, October, and February sampling dates were 39.9, 20.0, and 11.8%, respectively. Those are minimum estimates

[†]The fry moving past the last trap, T8, were included to estimate the total number of resident fry (6515).

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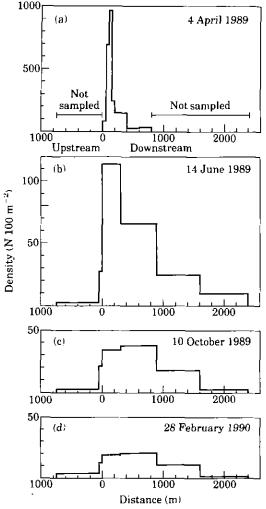


Figure 2. Estimated densities of fry and parr of Atlantic salmon at different distances from an artificial redd (0) during the early dispersal phase as estimated from trapping (a) and during successive electrofishing inventories (b, c, d).

because some emigration may have occurred during the period.

Discussion

We consider separately the fry and parr stages, since two different methods were used to make the population estimates and different factors may be involved to explain their distribution and movements.

Distribution of fry

The validity of estimates of number of fry drifting past the nets and settling at different distances from the redd depended on several assumptions. First of all, the experimental design to study the movements of fry following emergence was based on the assumption of passive drift. which meant that the fry would be randomly or uniformly distributed across the stream width and depth and that the catch of fry would be proportional to the flow. Each net filtered close to 5% of the flow and care was taken to place the trap on a transect with a flat bottom, where flow was smooth and devoid of obstacles provoking turbulences or eddy currents. The net opening allowed sampling of the whole water column. However, sampling may be biased if fry move actively downstream, and prefer, for instance, the banks rather than the midstream current. If this were the case in our experiment, sampling would underestimate population size since the nets were placed in the middle part of the stream. MacDonald (1960), studying the distribution of fry of four Oncorhynchus spp. in Williams Creek (British Columbia), found that sockeye (O. ncrka) and pink (O. gorbuscha) fry catches were related to water velocity, thus suggesting passive drift, whereas coho (O. kisutch) and chum (O. keta) appeared to prefer the sides of the river. In an artificial channel, Marty and Beall (1989) found no difference between captures of Atlantic salmon fry in nets filtering the same volume of flow along the banks or in the middle of the stream. Because of this, and of the way the nets were placed along transects in the Lapitxuri Brook, we feel that drifting or downstream moving fry were sampled representatively. This contention seems to be supported by the homogenous captures in the first three traps.

Another assumption concerning the estimates of drifting fry was that the freshet of 4 April, which interrupted trapping, occurred at the end of the dispersal phase immediately following emergence. If this phase was not terminated then survival to emergence and early dispersal would be underestimated, as well as the number of try settling between the nets. The shape of the daily capture distribution at trap I corresponds closely to that obtained during others experiments in the artificial channel (Marty and Beall, 1987, 1989) or in natural streams (Randall, 1982), presenting a single mode with about 95% of captures occurring within 12 to 15 days. We therefore conclude that the captures between 13 March and 4 April should cover well the emergence and early dispersal phases. Even if survival and fry densities are underestimated at this stage, the main conclusion that the majority of fry disperse within the first 2 weeks still stands. This is in agreement with the observation made in natural stream systems by Randall (1982), Hay (1989), Gustafson-Greenwood and Moring (1990). This downstream movement, as indicated by the captures in traps placed at different distances from the redd, was rapid and not just progressive. Fry covered 40-50 m per night in the first hundred metres, and some travelled 300 m or more within the same night. Downstream movement was also massive, with an estimated 91% of the surviving population settling within 400 m from the redd. A similar result was reported by Hay (1989) on the Girnock Burn, with fry observed 743 m downstream from an isolated redd. These observations contrast with those of several authors who note a colonization over a short distance. Egglishaw and Shackley (1973, 1980), Kennedy (1988), and Gustafson-Greenwood and Moring (1990) found that fry settled within 100 m downstream from the redd, and no further than 400–600 m. Following the first 2 or 3 weeks after emergence, the fry are supposed to be very sedentary with a weak capacity for dispersal (McCrimmon, 1954; Saunders and Gee, 1964; Symons, 1969; Bulleid, 1973; Le Gault and Lalancette, 1987).

In order to estimate the number of fry settling in the sections between traps, we made the assumption of negligible mortalities during this period. Some mortalities may have occurred during movement, but since dispersal was massive and rapid, and took place mostly during the night (Claireaux et al., 1993), predation must have been limited. Moreover, competition can be dismissed as a source of mortality at this stage because this dispersal occurred before the onset of territorial behaviour (Marty and Beall, 1989). The downstream moving fry were actively feeding and growing as shown by the change of weight samples, and not in a moribund state as the brown trout described by Elliott (1986) in Black Brows Beck.

The downstream movements of fry were not related to temperature (daily averages between 9 and 12.2°C) or discharge, which showed very little variation during the period 13 March-3 April. Emerging fry may be swept away by the current during swim-up since they do not vet possess full swimming capacities, and particularly if this occurs at night, when they may lose visual contact with the substratum. However, they are typically benthic organisms and do not usually swim away from the bottom (Beall et al., 1989). It is doubtful then that with current velocity averaging 0.6 m s⁻¹, well within the range of values found in redd and riffle areas, they would be carried passively as far as 200 or 400 m downstream. More research on fry behaviour at emergence is needed to understand the mechanisms of this initial downstream movement.

A change in juvenile distribution occurred between the spate on 4 April and the June census (Fig. 2), with the majority of salmon spreading from the 0-400-m zone to the 0-900-m, zone and many moving all the way to the confluence with the Nivelle 2400 m downstream. This change may have been caused by the spate, with many fry being swept away by the strong current. Mills (1964) found this to happen with hatchery-reared fry soon after release. However, the spate of 4 April was not very strong. Discharge increased from 0.4-0.5 m³ s⁻¹ in the preceding 3 weeks to 1.0 m³ s⁻¹ at the peak of the spate and average velocities from 0.6 to 0.75 m s⁻¹. Ottaway and Clarke (1981) and Crisp and Hurley (1991)

found that salmon fry had low rates of dispersal, between 0.25 and 0.7 m s⁻¹. In the Lapitxuri, there was some upstream movement during this period, indicating that fry displaced actively. Thus, the shift in density may have been the result of territorial competition which would occur at about this time after emergence (Kalleberg, 1958; Héland, 1971). Densities as high as 10 fry m⁻² were estimated over short distances near the redd (Fig. 2) just before the spate, and competition for space and feeding territories could be intense under these conditions. Interspecific competition was considered to be unimportant because very few trout juveniles were captured in the traps and during the June inventory.

Distribution of parr

In June, juvenile salmon densities near the redd had decreased to slightly over one individual m⁻², while densities in the 400-800-m zone increased from 0.35 to 0.65 individual m⁻². Another shift in distribution appeared during summer, with the levelling off of the highest densities near the redd and the formation of a mode in the 300-900-m zone, certainly due to densitydependent mortalities and out-migration (Mills, 1964). Elson (1957) found that hatchery parr released at high densities could migrate up to 800 m upstream from the release site and 1600 m downstream. During winter, upstream movements appeared to increase. In the Nivelle River, a large proportion of parr mature at 0+ (Dumas and Beall, unpublished data); adult salmon were released in the artificial channel upstream from the study area and spawned naturally in December 1989. Their activities may have attracted mature part via pheromones (Moore and Scott, 1991). Garcia de Leaniz (1989) found that mature male parr moved significantly more than immature male parr during the spawning season.

Growth and survival

Growth is usually rapid in our latitude. However, it was a little slower in the Lapitxuri than in the Nivelle proper (74 mm in October). It was comparable to that found in Brittany by Bagliniere and Maisse (1989) on a small tributary of the River Scorff (73 mm).

Minimum estimates of survival to emergence and early dispersal (51.9%) or to yearling parr (11.8%) fell within the range of high values cited by Bley and Moring (1988) for this species at similar stages. Survival during incubation to emergence was found to be much lower in the River Nivelle and quite comparable in an artificial stream located on the Lapitxuri Brook (Beall *et al.*, 1991). These results can be attributed to the good quality of the spawning habitat in the Lapitxuri and in the artificial stream.

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Acknowledgments

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References

- Baglinière, J. L., and Champigneulle, A. 1986. Population estimates of juvenile Atlantic salmon, Salmo salar, as indices of smolt production in the R. Scorff, Brittany. Journal of Fish Biology, 29: 467–482.
- Bagliniere, J. L., and Maisse, G. 1989. Dynamique de la population de juveniles de saumon atlantique (Salmo salar L.) sur un petit affluent du Scorff (Morbihan). Acta Oecologica, Oecologia Applicata, 10: 3-17.
- Beall, E., Heland, M., and Marty, C. 1989. Interspecific relationships between emerging Atlantic salmon. Salmo salar and coho salmon, Oncorhynchus kisutch, juveniles. Journal of Fish Biology, 35 (Suppl. A): 285-293.
- Beall, E., Marty, C., and Héland, M. 1991. Production de juvéniles de salmonidés pour le repeuplement, chenal de frai du Lapitxuri: Bilan 1981-1988. Rapport Convention d'étude Etat/INRA no. 2651 B, Station d'Hydrobiologie, Saint-Pée-sur-Nivelle. 55 pp.
- Bley, P., and Moring, J. R. 1988. Freshwater and oceanic survival of Atlantic salmon and steelhead: a synopsis, US Fish and Wildlife Service, Biological Reports, 88, 22 pp.
- Bulleid, M. J. 1973. The dispersion of hatchery-reared Atlantic salmon (Salmo salar) stocked into a fishless stream. International Atlantic Salmon Foundation. Special Publication Series, 4: 169-179.
- Claireaux, D., Beall, E., and Marty, C. 1993. Dispersal of salmonid juveniles at emergence in the Lapitxuri Brook, Basque Country, SW France. Poster presentation, Second Congrès Commun Limnologie-Océanographie, Evian (Haute-Savoie), 25-28 May 1993. (Résumé.)
- Crisp, D. T., and Hurley, M. A. 1991. Stream channel experiments on downstream movements of recently emerged trout, Salmo trutta L., and salmon, S. salar L. I. Effect of four different water velocity treatments upon dispersal rate. Journal of Fish Biology, 39: 347-361.
- Egglishaw, H. J., and Shackley, P. E. 1973. An experiment on faster growth of salmon, *Salmo salar* (L.), in a Scottish stream. Journal of Fish Biology, 5: 197-204.
- Egglishaw, H. J., and Shackley, P. E. 1980. Survival and growth of salmon, Salmo salur (L.), planted in a Scottish stream. Journal of Fish Biology, 16: 565-584.
- Elliott, J. M. 1986. Spatial distribution and behavioural movements of migratory trout, *Salmo trutta*, in a Lake District stream. Journal of Fish Biology, 55: 907-922.
- Elson, P. F. 1957. Using hatchery-reared Atlantic salmon to best advantage. Canadian Fish Culturist, 21: 7-17.

- Garcia de Leaniz, C. 1989. Site fidelity and homing of Atlantic salmon parr in a small Scottish stream. *In Salmonid migration and distribution symposium*, pp. 70-80. Ed. by E. Brannon and B. Jonsson. Contribution no. 979, School of Fisheries, University of Washington, Seattle.
- Gustafson-Greenwood, K. I., and Moring, J. R. 1990. Territory size and distribution of newly-emerged Atlantic salmon (Salmo salar). Hydrobiologia, 206: 125-131.
- Gustafson-Marjanen, K. I., and Dowse, H. B. 1983. Seasonal and diel patterns of emergence from the redd of Atlantic salmon (Salmo salar) fry. Canadian Journal of Fisheries and Aquatic Sciences, 40: 813–817.
- Hay, D. W. 1989. Effect of adult stock penetration on juvenile production of Salmo salar L. in a Scottish stream. In Salmonid migration and distribution symposium, pp. 93-100. Ed. by E. Brannon and B. Jonsson. Contribution no. 973, School of Fisheries, University of Washington, Seattle, June 1987.
- Héland, M. 1971. Observations sur les premières phases du comportement agonistique et territorial de la Truite commune (Salmo trutta L.) en ruisseau artificiel. Annales d'Hydrobiologie, 2: 33-46.
- Kalleberg, H. 1958. Observation in a stream tank of territoriality and competition in juvenile salmon and trout (Salmo salar L. and Salmo trutta L.). Reports of the Institute of Freshwater Research, Drottningholm, 32: 55-98.
- Kennedy, G. J. A. 1982. Factors affecting the survival and distribution of salmon (Salmo salar L.) stocked in upland trout (Salmo trutta L.) streams in N. Ireland. EIFAC technical paper (42), Suppl. Vol. 1: 227-242.
- Kennedy, G. J. A. 1988. Stock enhancement of Atlantic salmon (Salmo salar L.). In Atlantic salmon: planning for the future, pp. 345-373. Ed. by D. Mills and D. Piggins, Croom Helm, London.
- Le Cren, E. D. 1973. The population dynamics of young trout (Salmo trutta) in relation to density and territorial behavior. Rapports et Proces-Verbaux des Réunion du Conseil International pour l'Exploration de la Mer. 164: 241-246.
- Le Gault, M., and Lalancette, L. M. 1987. Observations sur le comportement d'alevins de saumons (*Salmo salar L.*) après leur déversement en rivière. Bulletin Français de Pêche et Pisciculture, 304: 32-40.
- McCrimmon, H. R. 1954. Stream studies on planted Atlantic salmon. Journal of the Fisheries Research Board of Canada, 11: 362–403.
- MacDonald, J. 1960. The behaviour of Pacific salmon fry during their downstream migration to freshwater and saltwater nursery areas. Journal of the Fisheries Research Board of Canada, 17: 655-676.
- Marty, C., and Beall, E. 1987. Rythmes journaliers et saisonniers de dévalaison d'alevins de Saumon atlantique à l'émergence. In La restauration des rivières à saumons, pp. 283-290. Ed. by M. Thibault and R. Billard. INRA, Paris.
- Marty, C., and Beall, E. 1989. Modalités spatio-temporelles de la dispersion d'alevins de Saumon atlantique (*Salmo salar L.*) à l'émergence. Revue des Sciences de l'Eau, 2: 831-846.
- Marty, C., Beall, E., and Parot, G. 1986. Influence de quelques paramètres du milieu d'incubation sur la survie d'alevins de Saumon atlantique (Salmo salar L.) en ruisseau expérimental. Internationale Revue der Gesamten Hydrobiologie, 71: 349-361.
- Mills, D. H. 1964. The ecology of the young stages of the Atlantic salmon in the River Bran, Ross-shire. Freshwater Salmon Fisheries Research, 32: 58 pp.
- Moore, A., and Scott, A. 1991. Testosterone is a potent odorant in male precocious Atlantic salmon (Salmo salar L.) parr. Philosophical Transactions of the Royal Society of London, B, 332: 241-244.

Ottaway, E. M., and Clarke, A. 1981. A preliminary investigation into the vulnerability of young trout (*Salmo trutta* L.) and Atlantic salmon (*S. salar* L.) to downstream displacement by high water velocities. Journal of Fish Biology, 19: 135-145

Randall, R. 1982. Emergence, population densities and growth of salmon and trout fry in two New Brunswick streams. Canadian Journal of Zoology, 60: 2259-2244.

Saunders, R. L., and Gee, J. H. 1964. Movements of young Atlantic salmon in a small stream. Journal of the Fisheries Research Board of Canada, 21: 27-36.

Seber, G. A. F., and Le Cren, E. D. 1967. Estimating population parameters from catches large relative to the population. Journal of Animal Ecology, 36: 631-643. Symons, P. E. K. 1969. Greater dispersal of wild compared with hatchery-reared juvenile Atlantic salmon released in streams. Journal of the Fisheries Research Board of Canada, 26: 1867-1876.

Vallières, A., and Dulude, P. 1990. Comparaison entre la reproduction naturelle, l'ensemencement de juvéniles et l'enfouissement d'oeufs de saumons atlantiques dans la rivière de l'Epaule, pp. 299-309. Ed. by N. Samson and J. P. Le Bel. Compte rendu de l'atelier sur le nombre de reproducteurs requis dans les rivières à saumons, Ile aux Coudres, février 1988. Ministère du Loisir, de la Chasse et de la Pêche, Direction de la Gestion des Espèces et des Habitats, Québec, 329 pp.